LONG-TERM DYNAMICS OF LARGE-BODIED FISHES ASSESSED FROM SPATIALLY INTENSIVE MONITORING OF A MANAGED DESERT RIVER

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ABSTRACT

Imperilment of native fishes worldwide, and particularly in the American Southwest, has prompted management actions to protect and recover threatened populations. Implementation of management activities, however, often proceeds without clear understandings of ecological interactions between native fishes and other biotic and physical components of the environment. Using data obtained in a 19-year, intensive monitoring effort across 288 km of the San Juan River in NM and UT, USA, we quantified relationships among large-bodied fishes and longitudinal environmental gradients, tested for faunal breaks of fishes and habitat structure along the river's course, and assessed the response of fishes to mechanical removal of non-native fishes and stocking of endangered fishes. Mesohabitat variation was not strongly linked to densities of large-bodied fishes, but we found strong and temporally consistent longitudinal patterns of native and non-native fishes: Native fish densities were highest upstream while non-native fish densities where highest downstream, potentially driven by differential responses to temperature regimes. Two breaks in the longitudinal structure of large-bodied fishes were identified and were associated with a man-made barrier and changes in the width of the river's floodplain. While densities of common native fishes were relatively constant during the study, non-native fish removal apparently reduced densities of one of two targeted species and densities of two endangered fishes increased as a result of stocking hatchery-reared fish. Results of this study suggest that large-bodied fishes of the San Juan River are responding to large-scale longitudinal gradients rather than small-scale habitat variation and management activities have altered densities of target species with limited responses by other fishes in the system. Copyright © 2014 John Wiley & Sons, Ltd.

INTRODUCTION

Native fishes worldwide have experienced unparalleled declines over the last century (Dudgeon *et al.,* 2006; Fullerton *et al.,* 2010), and almost 40% of North American fishes are currently endangered, threatened, or vulnerable (Jelks *et al.,* 2008). The highly endemic fishes in the Southwestern USA are exceptionally imperilled because of continued threats from water development, altered environmental flows, introduced species, and encroachment of invasive riparian vegetation (Minckley and Deacon, 1968; Holden and Stalnaker, 1975; Fagan *et al.,* 2002; Birken and Cooper, 2006; Nagler *et al.,* 2011; Franssen *et al.,* 2014a). Disentangling the spatial and temporal effects of changing environmental conditions on native fishes is difficult but requisite for effective conservation.

Long-term monitoring across multiple sites can help discriminate the relative influence of these effects by identifying when perturbations to a system occur and how they propagate through the system over space and time (e.g. Propst *et al.,* 2008).

The long-term modification of fish assemblages in the American Southwest (Miller, 1961; Olden and Poff, 2005) has prompted numerous management actions, with varying success, to protect and recover native fish populations in the Colorado River basin. Realization of deleterious effects of altered flow regimes has increased management of stream flows in impounded systems to benefit native species (Valdez *et al.,* 2001; Propst and Gido, 2004; Gido and Propst, 2012). However, it is often difficult to assess contributions of flow management to ecosystem restoration (Konrad *et al.,* 2012), and little information exists on how advantageous flow manipulations may be to native fishes in the Colorado River basin. Other management strategies have included stocking hatchery-reared federally protected fishes (Schooley and

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Marsh, 2007; Zelasko *et al.,* 2010) and mechanical removal of non-native fishes (Tyus and Saunders, 2000; Mueller, 2005; Coggins *et al.,* 2011; Franssen *et al.,* 2014b; Propst *et al.,* 2014). Although management activities aim to protect or recover native fishes, these efforts operate under the assumption that potentially complex interactions among native and non-native fishes in heavily altered systems are well understood and predictable (Mueller, 2005). Riverine systems, however, have strong, and often complex, spatial gradients that occur along the river continuum (Vannote *et al.,* 1980; Fausch *et al.,* 2002).

Abiotic environmental conditions largely dictate which fish species can persist in different aquatic systems (Jackson *et al.,* 2001), and longitudinal environmental variation along a river's course can strongly influence faunal structure (Horwitz, 1978; Vannote *et al.,* 1980). Fish assemblages typically transition from headwaters with a few specialist species to larger mainstem reaches with higher species richness and an increased diversity of morphologies and life history strategies (Rahel and Hubert, 1991). Longitudinal variation in abundance of species is likely the product of interactions among species-specific ecologies and gradients in biotic and physical components of the environment (Matthews, 1998; Ross, 2013). The ability of non-native fishes to successfully invade communities is also dependent on their ability to withstand environmental conditions in recipient systems, which might vary with longitudinal environmental conditions. Studies of invaded streams in California, USA, demonstrated that while biotic interactions affected the spatial distribution of native and non-native fishes, longitudinal variation in stream conditions were also important factors (Moyle and Light, 1996; Marchetti and Moyle, 2001; Moyle and Marchetti, 2006). Identifying how the structure of non-coevolved fish assemblages are altered by varying habitat types or along environmental gradients may be particularly useful for identifying longitudinal faunal breaks that may serve as manageable stream units (Fausch *et al.,* 2002; Ibarra *et al.,* 2005; Lasne *et al.,* 2007).

Temporal variability in stream conditions can influence structure of non-coevolved fish assemblages, but these ecological dynamics may only be evident over long periods of time. Long-term monitoring of communities can provide benchmarks for natural variability of assemblages (Grossman *et al.,* 1990), help detect lagged responses to extreme events (e.g. flood, drought) (Franssen *et al.,* 2006; Magalhaes *et al.,* 2007), and may be particularly important for identifying anthropogenic versus natural drivers of ecological change (Magurran *et al.,* 2010). For example, variation in the timing, velocity, and volume of annual stream discharge can differentially impact the density and distributions of native and non-native fishes (Moyle and Light, 1996; Marchetti and Moyle, 2001; Propst and Gido, 2004; Gido and Propst, 2012; Kiernan *et al.,* 2012), revealing that native and non-native

fishes may have dissimilar responses to temporal environmental variation.

While the density of stream fishes may correlate with spatial and temporal environmental gradients, the spatial distribution of fishes may also be dictated by local habitat conditions at various scales (Matthews, 1998; Fausch *et al.,* 2002; Ross, 2013). Different stream fishes and age classes can select or partition habitats to lower intraspecific and interspecific competition or reduce predation pressure (Ross, 1986; Schlosser, 1987). Thus, effects of invasive fishes on native communities will likely be mediated by habitat overlap between native and non-native fishes and deleterious effects may be minimalized if they spatially or temporally occupy different habitats (Ayala *et al.,* 2007).

Herein, we used a spatially and temporally intensive data set to quantify dynamics of the native and non-native large-bodied fishes of the San Juan River, NM and UT, USA. We were particularly interested in assessing the effects of longitudinal environmental gradients and habitat associations of native and non-native fishes, identifying longitudinal faunal and habitat breaks along the river's course and quantifying temporal trends in fish densities as they might be mediated by management activities. Because of the disparity in evolutionary histories and ecologies of native and non-native fishes and their differential response to environmental gradients, we predicted that large-bodied fishes would demonstrate strong longitudinal patterns in their abundance. Additionally, we predicted that most changes to fish populations would be driven by management activities associated with non-native fish removal and stockings of federally protected fishes.

MATERIALS AND METHODS

Study site

The San Juan River, a partially regulated tributary of the Colorado River, exhibits considerable longitudinal environmental variation through its course from the San Juan Mountains of south-west Colorado across the high desert of north-west New Mexico and south-east Utah before entering Lake Powell (Figure 1). The median annual discharge between 1935 and 2013 was 51.5 m^3/s [US Geological Survey (USGS) gauging station 09368000]. Prior to the impoundment of the San Juan River by Navajo Dam in 1962, the river flowed unimpeded about 484 km to its confluence with the Colorado River in the area now inundated by Lake Powell (Figure 1). Over the past century, 19 non-native fishes (mostly small bodied) have invaded the San Juan River (Ryden, 2000), exceeding the river's historical fish fauna of up to eight native species (Tyus *et al.,* 1982), two of which are federally protected. The river was impounded in 1962, creating Navajo Reservoir (NM and CO), which drastically altered stream habitats and temperatures below the dam
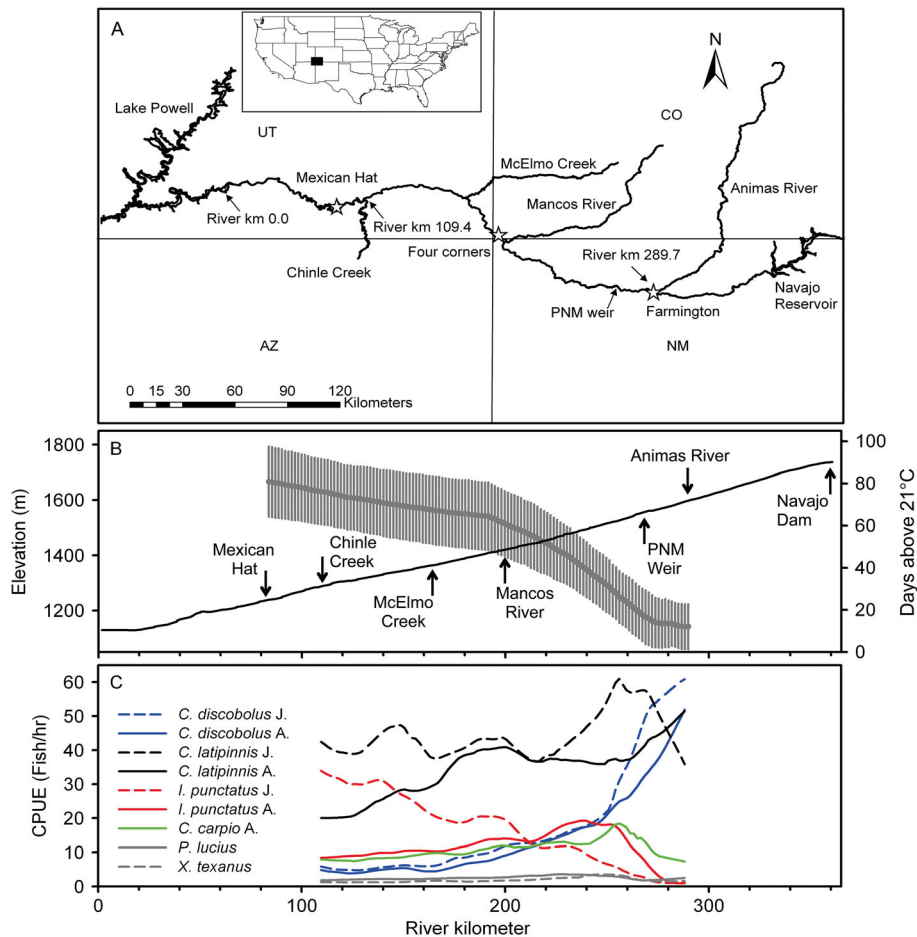
Figure 1. Map of study area on the San Juan River (A). Locations of notable features are demarcated. Panel (B) shows longitudinal variation in river elevation (metres above sea level) and the mean (±1 S.D.) numbers of days each 1.6 Rkm experienced mean daily temperature of ≥21°C. Panel (C) demonstrates the longitudinal mean CPUE for each species/age class over the entire study period of the large-bodied fishes used in analyses. Juvenile and adult groups are denoted with (J.) and (A.), respectively. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

through hypolimnetic water releases and intensified the river's longitudinal thermal gradient. While the impoundment fragmented and truncated stream reaches available for native fishes, the dam also modified the river's natural flow regime by lowering historical annual spring discharge and elevating summer flows (Franssen *et al.,* 2007). Additionally, channel complexity in the San Juan River has been reduced by anthropogenic straightening the main channel and riverwide encroachment of invasive salt cedar (*Tamarix* spp.) and Russian olive (*Elaeagnus angustifolia*). Similar to other rivers in the Colorado River basin (Birken and Cooper, 2006; Nagler *et al.,* 2011), encroachment of salt cedar and Russian olive has likely confined, narrowed, and reduced braiding of the San Juan River's mainstem compared with historical conditions (Stromberg *et al.,* 2007; Franssen *et al.,* 2014a).

Federal listing status of two large-bodied native fishes (Colorado pikeminnow *Ptychocheilus lucius* and razorback sucker *Xyrauchen texanus*) prompted multiple management activities to recover their populations and lower densities of

non-native fishes in the San Juan River. Population restoration efforts via stocking age-0 (i.e. young of year) P. lucius and subadult and adult X. texanus began in the mid 1990s and continues today. Reservoir releases have been managed since 1998, when possible, to mimic the timing, duration, and magnitude of a natural flow regime to increase the abundance of federally protected species and decrease densities of non-native fishes (Propst and Gido, 2004; Gido and Propst, 2012). Large-scale and intensive non-native fish removal efforts began in the early 2000s to reduce densities of introduced common carp (*Cyprinus carpio*) and channel catfish (*Ictalurus punctatus*), which numerically comprised 9 and 13%, respectively, of the total large-bodied fishes collected in the late 1990s.

Spatial and temporal fish assemblage variation

Annual large-bodied fish surveys were conducted via raft-mounted electrofishing between 1994 and 2012 during

autumn (September or October) base flow. During these surveys, two electrofishing rafts sampled each shoreline of the river in tandem and the number of fish and seconds from both rafts were summed at the ends of each 1.6 river km (Rkm), but only three of every four 1.6 Rkms were sampled most years (all Rkms were sampled 1994–1998). Fish species were divided into juveniles and adults as follows: non-native juvenile *I. punctatus* were ≤300 mm TL, native juvenile bluehead sucker (*Catostomus discobolus*) ≤300 mm TL, native juvenile flannelmouth sucker (*Catostomus latipinnis*) ≤410 mm TL, and all larger individuals were considered adults. Juvenile *C. carpio* were only rarely encountered, so only adult *C. carpio* ≥250 mm TL were included for study. Because of low numbers of adult *P. lucius* and juvenile *X. texanus* encountered during the study period, these species were not divided into age classes. Because raft-mounted electrofishing is likely inefficient at collecting smaller fish, only large-bodied fish were included in analyses.

Spatial and temporal mesohabitat variation

Available mesohabitats (based on velocity, depth, and direction of flow) were quantified in every Rkm (109.4–289.7) between 1994 and 2007. Aerial videography was collected each September or October (2002 data were collected in July) when the river was at base flow. The river was then floated via raft and five general mesohabitat types: riffle, run, shoal, pool, and low velocity were delineated on the aerial photographs. The area (m^2) of each habitat type in every 1.6 Rkm was then quantified using GIS software.

Spatial and temporal temperature variation

Spatial and temporal variation in water temperature was quantified to assess the relationship between thermal gradient and longitudinal variation in fish assemblages. Between 1994 and 2012, mean daily temperature was recorded at three locations (Farmington, Four Corners, and Mexican Hat; Figure 1) using Onset Computer Corporation (Bourne, MA, USA) HOBO water temperature loggers that recorded data every 15 min. Data were downloaded and checked for errors two to four times per year. To quantify spatial variation in water temperature, we interpolated mean daily water temperature for each 1.6 Rkm assuming a linear increase/decrease in temperature between adjacent temperature loggers for a given day. For each year, we calculated the number of days each RM in the study area (i.e. Rkm 109.4–289.7) experienced mean daily temperature ≥21°C as a measure of thermal gradient (temperatures <21°C are known to limit *I. punctatus* growth and recruitment; Patton and Hubert, 1996).

DATA ANALYSES

Spatial and temporal fish assemblage variation

Prior to all analyses, fish CPUE were $log_{10}(x+1)$ transformed to reduce the effects of abundant species. Additionally, only species/size classes that occurred in at least 10% of 1.6 Rkm samples were included in analyses. To summarize spatial and temporal variation in fishes, we conducted a principal component analysis (PCA) based on a correlation matrix of samples. We chose PCA because of observed linear changes in species abundance and minimal species turnover. Only axes with eigenvalues >1.0 were retained for interpretation. To assess spatial and temporal trends in large-bodied fishes, we averaged PC scores for each axis by each 1.6 Rkm and year. We used Pearson's *r* to test for correlations between mean PC scores and Rkm and year.

Spatial and temporal mesohabitat variation

The total area (m^2) of each mesohabitat within each 1.6 Rkm was $log_{10}(x+1)$ transformed to reduce the effects of the most abundant mesohabitat types and summarized spatial and temporal trends using PCA as described in the preceding texts.

Longitudinal zonation of fishes and mesohabitats

We used multivariate regression tree analysis (MRT), which is often used to detect breaks or groups in a multivariate data set along a univariate or multivariate gradient (De'ath and Fabricius, 2000), to identify specific locations along the river that represented changes in assemblage structure for each year of the study. Multivariate regression tree analysis calculates the within-group sums of squares for a subset of cases in the dependent variables (i.e. large-bodied fishes) created by a split made at every cut-point along an explanatory variable (i.e. Rkm). The split in the explanatory variable that minimizes the total sums of squares of both subsets is retained as the first node or split. This same process is then repeated for each new subset defined by the previous split. To assess spatial and temporal variation in longitudinal zonation of mesohabitats, similar in the preceding texts, we conducted MRT using the area of each mesohabitat type within each 1.6 Rkm as the dependent variables and Rkm as the explanatory variable. We conducted MRT on each year separately and then summarized the number of splits occurring along the river during the study period. We conducted MRT using the mvpart function in the MVPART package in the R statistical language (R Development Core Team, 2011).

Spatial and temporal environmental correlates of large-bodied fishes

We assessed spatial and temporal environmental variables that correlated with large-bodied fishes during the study period using redundancy analysis (RDA). Redundancy analysis is a direct gradient technique (or constrained ordination) that consists of a series of multiple linear regressions followed by a PCA of the fitted values (Legendre and Legendre, 1998). We limited our RDA analysis between 1994 and 2007 because habitat data were only available in those years. Fish CPUE (fish/h) were entered as dependent variables while area of mesohabitat types, days $\geq 21°C$, Rkm, mean annual discharge (Q), and year (as a covariate) were explanatory variables. Mean annual discharge (Q) was quantified from the USGS gauging station at Shiprock, NM (gauge 09368000). We used a stepwise selection procedure to choose the explanatory variables with the strongest associations with large-bodied fishes using the step function from the package stats in R. We tested for the significance of each variable and each RDA axis in the final RDA model using 1000 permutations (anova function in R).

RESULTS

Spatial and temporal fish assemblage variation

Three PC axes explained 68% of the variance in large-bodied fishes (Table I). The first axis explained 29% and was positively associated with juvenile and adult *C. discobolus* and negatively associated with juvenile *I. punctatus.* This axis largely reflected longitudinal variation of densities of these fishes (Figure 2A). The second axis explained 24% of the variance and reflected temporal variation in large-bodied fishes; *P. lucius* and *X. texanus* were positively associated and *C. carpio* was negatively associated with PC II (Figure 2B). The third axis explained 16% of the variance and was positively associ-

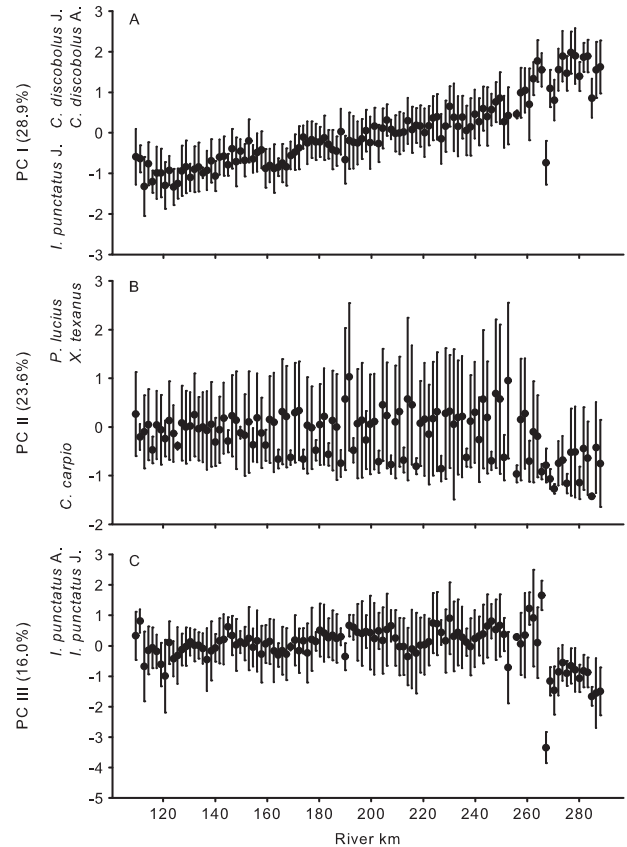Figure 2. Mean (±1 S.D.) PC axis I‑III (A‑C) scores grouped by 1.6 Rkms. Species/age classes with loadings with absolute values >0.5 are denoted on the *y*-axes

ated with juvenile and adult *I. punctatus*, which demarked a strong shift in the CPUE of these fishes near PNM weir at Rkm 268 (Figure 2C). Correlation analyses revealed significant correlations between Rkm and PC I, generally showing increases of juvenile and adult *C. discobolus* and decreases in juvenile *I. punctatus* moving upstream (Table II; Figure 2A). PC II also had significant correlations with Rkm but was much more strongly correlated with year (Table II; Figure 3B), capturing temporal increases in *P. lucius* and *X. texanus* and decreases of *C. carpio*. There was no significant relationship between PC III and Rkm, but this axis illustrated the abrupt decline in *I. punctatus* upstream of a weir (PNM weir) rather than a longitudinal gradient.

Spatial and temporal mesohabitat variation

Only two PC axes were retained from the PCA of mesohabitat types and together explained 51% of the variance (Table III). The first axis explained 27% of the variance and was positively associated with shoal and riffle mesohabitats (Figures 4A and 5A). The second axis explained 24% of the variance in mesohabitat types and was positively associated

Table I. The percent of variance explained by each axis and loadings from PCA summarizing variation in CPUE of fishes/age classes collected during the study period

Species/Age	PC I (28.9%)	PC II (23.6%)	PC III (16.0%)
C. discobolus J.	0.86	0.04	0.13
C. discobolus A.	0.84	−0.02	0.13
C. latipinnis J.	0.39	0.29	0.50
C. latipinnis A.	0.59	−0.16	0.43
I. punctatus J.	−0.67	0.29	0.53
I. punctatus A.	−0.39	0.30	0.70
C. carpio A.	−0.04	−0.72	0.43
P. lucius	0.10	0.86	−0.09
X. texanus	0.22	0.76	−0.07

Juvenile and adult age classes are denoted with 'J.' and 'A.', respectively.

Table II. Results from Pearson correlation analyses testing relationships among Rkm and year and mean PC scores averaged by Rkm and year for large-bodied fishes and mesohabitat features

		PC I	PC II	PC III
Fishes	Rkm	0.908**	−0.311**	−0.180
	Year	0.374	0.921**	−0.432
Mesohabitat	Rkm	−0.286**	−0.524**	
	Year	0.542*	−0.729**	

Significance levels are denoted with:
**$p < 0.001$
*$p < 0.05$.

Table III. The percent of variance explained by each axis and loadings from PCA summarizing variation in the area of each mesohabitat type in each 1.6 Rkm between 1994 and 2007

Mesohabitat	PC I (26.6%)	PC II (23.5%)
Run	0.18	0.82
Riffle	0.71	−0.44
Low velocity	0.23	0.52
Pool	0.41	−0.15
Shoal	0.75	0.15

with run and low-velocity mesohabitat types and negatively associated with riffles (Figure 4B). There were weak, but significant, negative correlations between mean PC I scores and Rkm and year; however, these correlations were likely influenced by several outliers (Table II). Stronger correlations were found between PC II and Rkm and year indicating an increase in riffle mesohabitats over time and moving upstream.
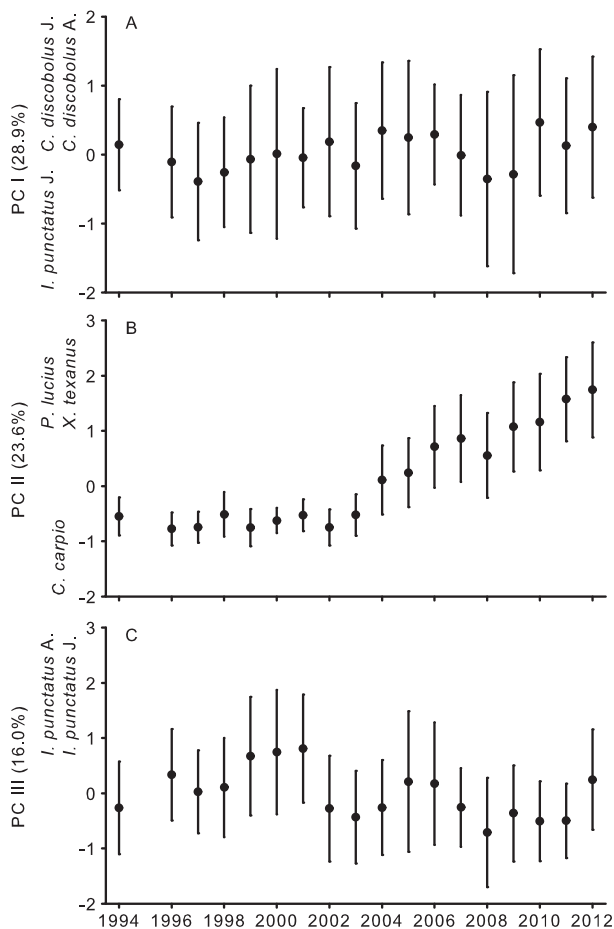
Longitudinal zonation of fishes

Multivariate regression tree analyses explained an average of 62% (range = 43–78%) of the variance in longitudinal variation (faunal breaks) in large-bodied fishes among years, and all trees demonstrated more than one split (Figure 6). In 10 of 18 years, primary splits were between Rkm 247.8 and 267.2. The remaining eight primary splits were between Rkm 188.3 and 214.0. Weaker secondary splits generally occurred in these same regions, but higher order splits exhibited more longitudinal variation.
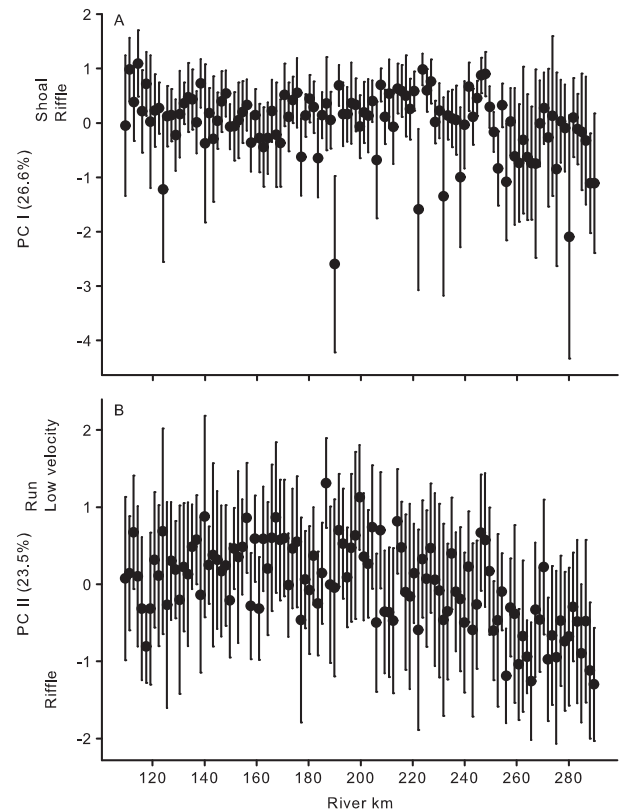

Figure 3. Mean (±1 S.D.) PC axis I‑III (A‑C) scores grouped by year. Species/age classes with loadings with absolute values >0.5 are denoted on the y-axes

Figure 4. Mean (±1 S.D.) PC axis I‑II (A‑B) scores grouped by 1.6 Rkms. Mesohabitat types with loadings >0.5 (absolute value) are denoted on the y-axes
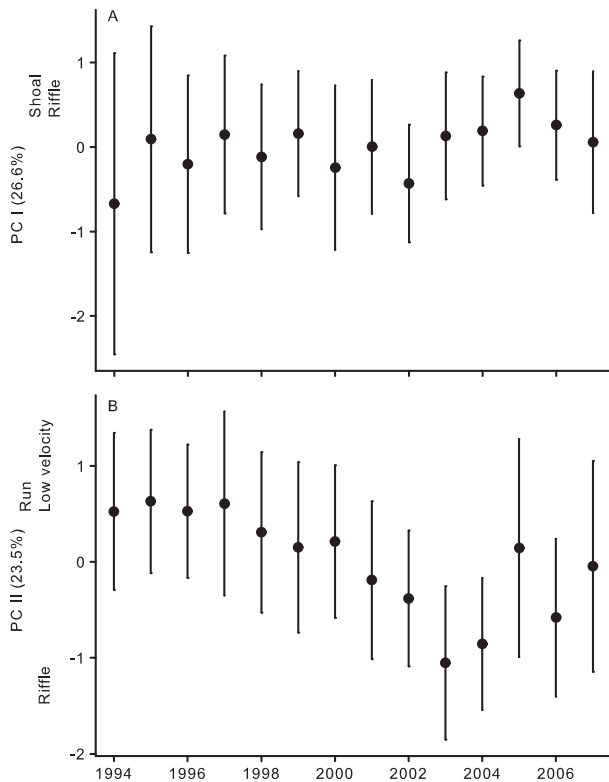
Figure 5. Mean (±1 S.D.) PC axis I-II (A-B) scores grouped by year. Mesohabitat types with loadings >0.5 (absolute value) are denoted on the *y*-axes
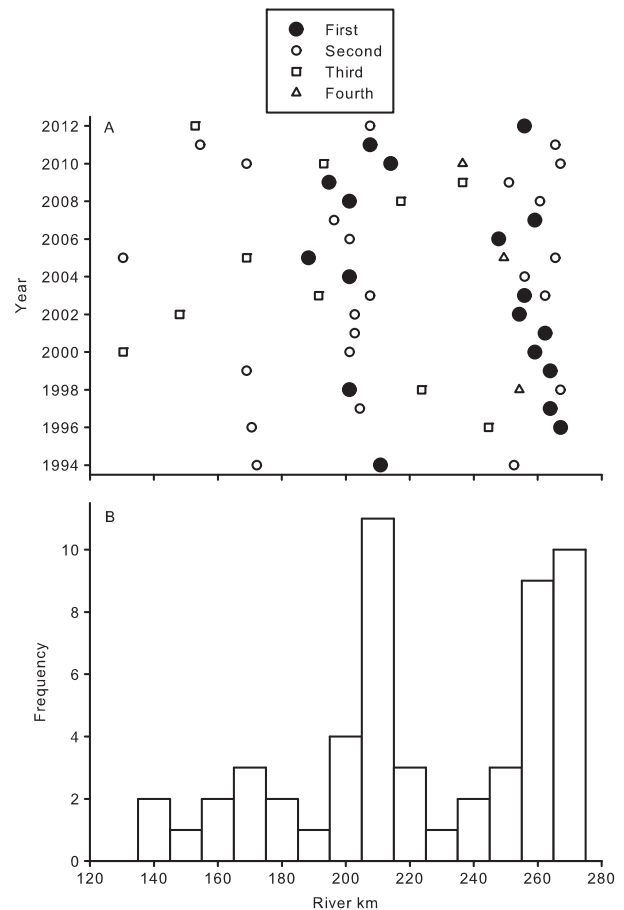

Figure 6. Graphical summary of results from multivariate regression tree analyses assessing longitudinal zonation of fishes each year (A). Symbols represent breaks identified from each pruned regression tree each year. The histogram below quantifies the number of breaks located along each 16.1 Rkm bin during the study period (B)

Longitudinal zonation of mesohabitats

Longitudinal zonation of mesohabitats was not as demarcated as those observed in large-bodied fishes. On average, MRT explained 14% of the variance (range = 5–29%) in longitudinal mesohabitat variation and all trees contained only one or two splits. The majority of primary splits occurred between Rkm 244.6 and 255.9 and between Rkm 149.7 and 181.9 (Figure 7). The three secondary splits occurred at Rkms 284.9, 170.6, and 135.2.

Spatial and temporal environmental correlates of large-bodied fishes

The RDA retained all explanatory variables except the run mesohabitat type, and Rkm explained the most variation by a large margin in the final model (Table IV). The first five RDA axes were significant; however, only the first three axes explained more than 1% of the variation in correlations between the explanatory variables and large-bodied fishes (RDA I = 39%, RDA II = 6%, RDA III = 3%). The first axis was strongly associated with longitudinal variation: positively with Rkm and negatively with days ≥21°C (Figure 8). Juvenile and adult *C. discobolus* were positively associated with this axis while juvenile *I. punctatus* were negatively associated,

indicating a strong longitudinal pattern in their densities. The second axis was largely associated with year and positively associated with adult *I. punctatus*. The third axis was positively associated with low velocity, riffle, and shoal mesohabitats as well as *C. carpio* and adult *I. punctatus* and was negatively correlated with year and pool mesohabitats.

DISCUSSION

Long-term and spatially intensive monitoring identified strong patterns of both spatial and temporal variation in the abundance of large-bodied fishes. Much of the longitudinal variation was because of higher densities of juvenile and adult *C. discobolus* (and, to a lesser extent, adult *C. latipinnis*) upstream as well as higher densities of juvenile *I. punctatus* downstream. Osmundson *et al.* (2002) revealed a comparable pattern with *C. discobolus* and *C. latipinnis* in the Colorado River and
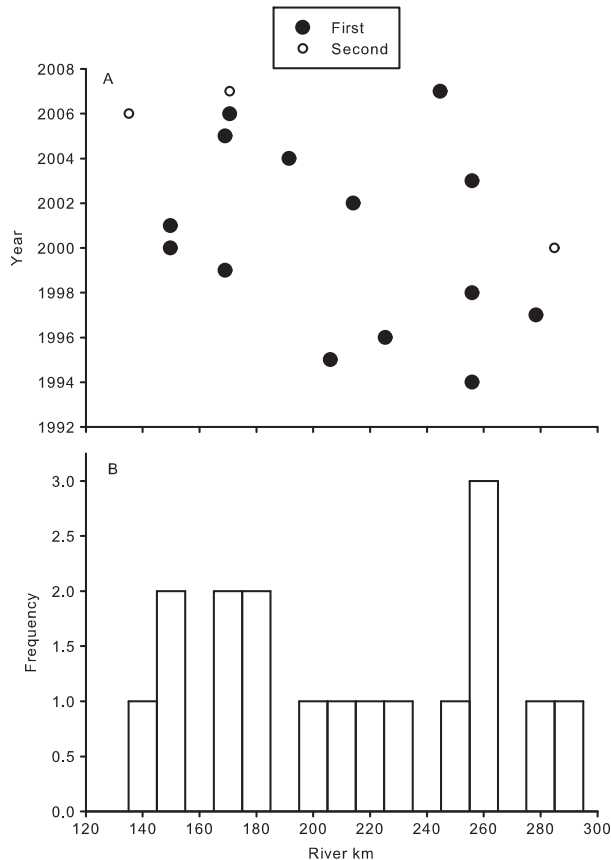
Figure 7. Graphical summary of results from the multivariate regression tree analyses assessing longitudinal breaks in habitats each year (A). Symbols represent breaks identified from each pruned regression tree each year. The histogram below quantifies the number of breaks located along each 16.1 Rkm bin during the study period (B)

Table IV. Results from a permutation procedure testing the significance of each variable in the final RDA model correlating these variables with densities of large-bodied fishes

Variable	R^2	F	p
Rkm	36.4	448.9	0.001
Year	5.0	61.2	0.001
Days ≥21°C	4.1	50.2	0.001
Q	1.5	18.8	0.001
Shoal	0.6	8.0	0.001
Riffle	0.4	5.0	0.003
Low velocity	0.2	2.7	0.038
Pool	0.2	2.3	0.050

Only significant variables were retained in the final model.

Navajo dam not only diminished river temperature but also reduced fine sediment loads in the river, lending to potentially lower turbidity in upstream reaches, which would also help increase in-stream production (Ward and Stanford, 1983; Aristi *et al.,* 2014). Nevertheless, several tributaries along the river
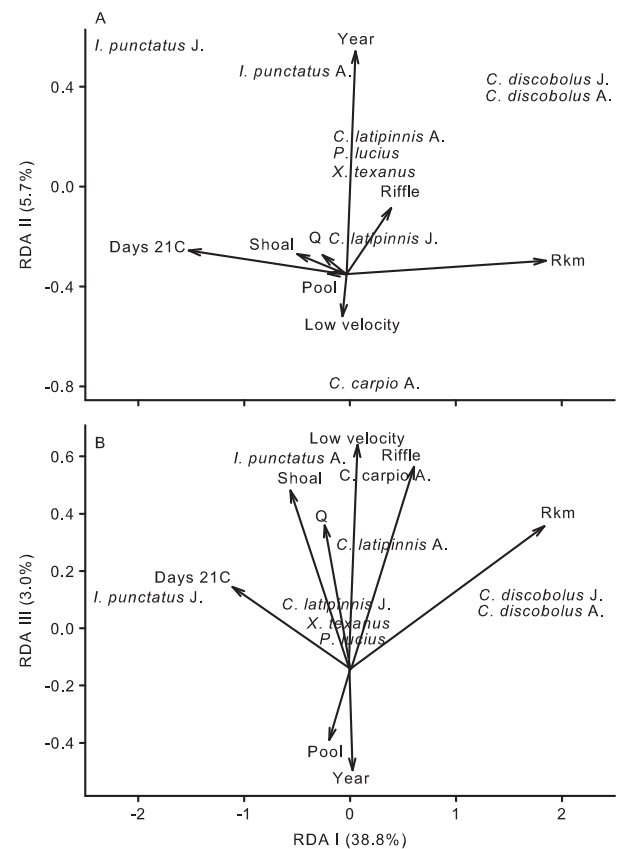
showed that higher densities of these fishes correlated with increased riffle mesohabitats, primary and secondary production, and lower amounts of fine sediment. Similarly, a pattern of higher native fish densities upstream with cooler water temperature, greater canopy cover, fewer pools, and increased flow compared with higher non-native fish densities downstream with the opposite environmental conditions were found in an invaded California stream system (Marchetti and Moyle, 2001). While many environmental conditions covary along the river course (Vannote *et al.,* 1980), gradients in productivity, habitat, and temperature likely contributed to the spatial distribution of fishes in the San Juan River. Mesohabitat variation along the river course generally demonstrated more riffle and fewer run mesohabitats upstream compared with downstream. Similar to the Colorado River (Osmundson *et al.,* 2002), greater autochthonous productivity in riffle mesohabitats with shallower water in upper reaches of the San Juan River likely facilitated higher densities of herbivorous/insectivorous *C. discobolus* and *C. latipinnis*. Hypolimnetic releases from

Figure 8. Results of redundancy analysis correlating environmental, spatial, and temporal variables: Rkm, days ≥21°C, year, and mesohabitat with fishes in the San Juan River between 1994 and 2007. The top panel (A) plots RDA I versus RDA II while the bottom panel (B) plots RDA I versus RDA III

course contributed fine sediments that likely reduced autochthonous productivity in a downstream direction and might explain the lower native catostomid densities in downstream reaches.

Thermal niches among species could also mediate the longitudinal distribution of native catostomids and non-native *I. punctatus*. Most native fishes in the Colorado River basin were displaced from reaches immediately below dams by hypolimnetic releases (e.g. Vanicek, 1970; Schmidt *et al.,* 1998). The same temperature gradient may also limit the upstream distribution of non-native juvenile *I. punctatus*. *I. punctatus* generally do not spawn until water temperatures reach 21.0°C (Small and Bates, 2001), and juveniles have preferred temperatures of 29.0°C in lab settings (Díaz and Bückle, 1999) and optimum field-measured temperatures between 30.0 and 35.0°C (Layher and Maughan, 1985). In addition, both juveniles and adults show relatively slow growth at temperatures <21.0°C (Andrews *et al.,* 1972). Although *I. punctatus* may spawn in tail waters of reservoirs, age-0 individuals show extremely low survivorship linked to extended periods with water <21.0°C during the growing season (Patton and Hubert, 1996). Therefore, the strong upstream/downstream distribution of juvenile *I. punctatus* is potentially mediated through water temperature where downstream reaches with warmer water facilitate higher juvenile survival and growth whereas upstream reaches are occupied by larger/older individuals that may be selecting reaches with higher productivity but lower than optimum temperature. Indeed, upstream reaches of the river tend to have higher productivity and macroinvertebrate densities compared with downstream reaches (Bliesner and Lamarra, 2000). Although lower water temperatures upstream potentially lower growth rates of *I. punctatus*, reaches higher in the river are more productive, and their occupancy is thus an acceptable trade-off. While temperature may limit the upstream distribution of *I. punctatus*, both native catostomids had their highest densities upstream, suggesting that they have greater tolerance for cooler water and also benefit from higher productivity in these reaches.

Assessment of longitudinal zonation of fishes revealed two relatively consistent breaks in large-bodied fishes along the river course. The first and strongest break (evidenced by the frequency of primary splits) occurred between Rkm 247.8 and 267.2 while a second series of breaks occurred between Rkms 193.1 and 209.2. These faunal breaks were associated with longitudinal breaks in mesohabitats (Rkm 241.4 and 257.5 as well as between RM 160.9 and 177.0), but environmental breaks explained considerably less variation in mesohabitats compared with faunal breaks. While fishes may be responding to variation in mesohabitat availability, other factors likely contributed to the longitudinal zonation of large-bodied fishes. The PNM weir located at Rkm 268.1 represented a clear faunal transition by imposing a barrier to upstream fish movement. A selective fish passage was constructed in 2002 and operated during spring and summer months to allow migration of native fishes upstream of the weir while ostensibly precluding non-native fish passage. This structure likely enabled upstream passage of low numbers of *I. punctatus*. Although densities of adult *I. punctatus* decline sharply in the RM immediately below the weir, juvenile densities decrease longitudinally from downstream to upstream to the weir (Figure 1A). Indeed, all fauna breaks occurred downstream of PNM weir. The second faunal break downstream was also not associated with the breaks in mesohabitats we measured; however, this area is where the river's floodplain substantially narrows (Bliesner and Lamarra, 2000). Thus, it appears that other environmental gradients also contribute to breaks in large-bodied fishes but were not strongly associated with the mesohabitats we quantified.

Temporal variation in large-bodied fishes was linked to increased densities of federally protected *P. lucius* and *X. texanus* and lower densities of non-native *C. carpio* over the study period. Following our prediction, recent management efforts via stockings increased the densities of endangered fishes. Age-0 *P. lucius* and juvenile and adult *X. texanus* have been stocked annually since the mid 1990s and continues today. While stockings have increased the numbers of these fishes in the river, the low abundance or absence of juveniles of these species in small-bodied fishes monitoring suggest that recruitment of naturally spawned fish in the river is extremely low (Franssen *et al.,* 2014a). Thus, the increased abundances of juveniles and adults were the result of more stocked individuals surviving in the river rather than natural recruitment. In addition to increased densities of stocked fishes, non-native *C. carpio* experienced precipitous declines during the study period. A non-native fish removal program was most likely responsible for the declines of *C. carpio* (Franssen *et al.,* 2014b). However, the non-native removal program has been not been as successful in reducing densities of *I. punctatus*, likely because, in part, they are less susceptible to electrofishing capture than *C. carpio*. While the non-native fish removal efforts measurably diminished *C. carpio*, there was no evidence that juvenile and adult catostomids responded positively (this study, Franssen *et al.,* 2014b).

Longitudinal and temporal trends in mesohabitat were likely associated with the establishment of salt cedar (*Tamarix* spp.) and Russian olive (*E. angustifolia*) along much of the San Juan River's banks and long-term effects of regulated flows and impoundment. Similar to other rivers in the Colorado River basin (Birken and Cooper, 2006; Nagler *et al.,* 2011), encroachment of *Tamarix* and *E. angustifolia* has confined and narrowed the San Juan River's mainstem channel compared with historical conditions. Contraction of river channel reduces overall habitat complexity and diminishes suitability of habitats for stream fishes (Shields *et al.,* 1994; Franssen *et al.,* 2014a). The reservoir reduced the amounts of fine sediments available to reaches

below the dam (Kondolf, 1997; Ibanez *et al.,* 1998), increasing the coarseness of substrates that potentially facilitated development of more riffle mesohabitat (Gordon *et al.,* 2004). Reduced spring flows also might contribute to lower channel complexity by decreasing out of bank flows that were likely important for historical channel formation. Nonetheless, any spatial and temporal trends in riffle mesohabitat types during the study period were not followed by spatial changes in the large-bodied fishes, suggesting that mesohabitat types are not strongly selected by these fishes or are not a limiting factor in their distributions. Flow management to maximize water storage for agricultural and municipal consumption reduced the frequency and volume of flows capable of causing major channel realignment. Consequently, mesohabitat creation and loss dynamics were altered but with unknown effects on large-bodied fishes.

Our study period encompassed extremely low (2002) and high (1999) years of discharge. While annual flow variation can have a strong influence on the abundance of small-bodied native and non-native fishes in the San Juan River (Propst and Gido, 2004; Gido and Propst, 2012), mean annual discharge had little impact on the spatial and temporal variation of large-bodied fishes. Weak influences of annual discharge on large-bodied fishes are not surprising given the ability of these fishes to resist being displaced by high flows and their longevity.

Native fishes in the Colorado River basin will likely continue to face deleterious anthropogenically driven changes to environmental conditions into the future. Spatially intensive sampling of 180 Rkm over 19 years allowed a high-resolution understanding of how fishes responded to environmental gradients that are largely influenced by anthropogenic activities. In particular, spatial patterns were associated with thermal and mesohabitat gradients that are influenced by impoundments as well as invasive riparian vegetation. Intensive management, including stocking and non-native fish removals resulted in strong temporal trends. This long-term data set illuminated species responses to environmental conditions and indicated somewhat successful management strategies (i.e. stocking of endangered fishes and removal of *C. carpio*) as well as significant challenges (in-stream obstructions, removal of *I. punctatus*, and limited recruitment of threatened fishes). Continued monitoring of this system and expanding our understanding of its functioning over time will provide additional insights necessary to improve conservation prospects for native fish assemblages in the American Southwest and elsewhere.

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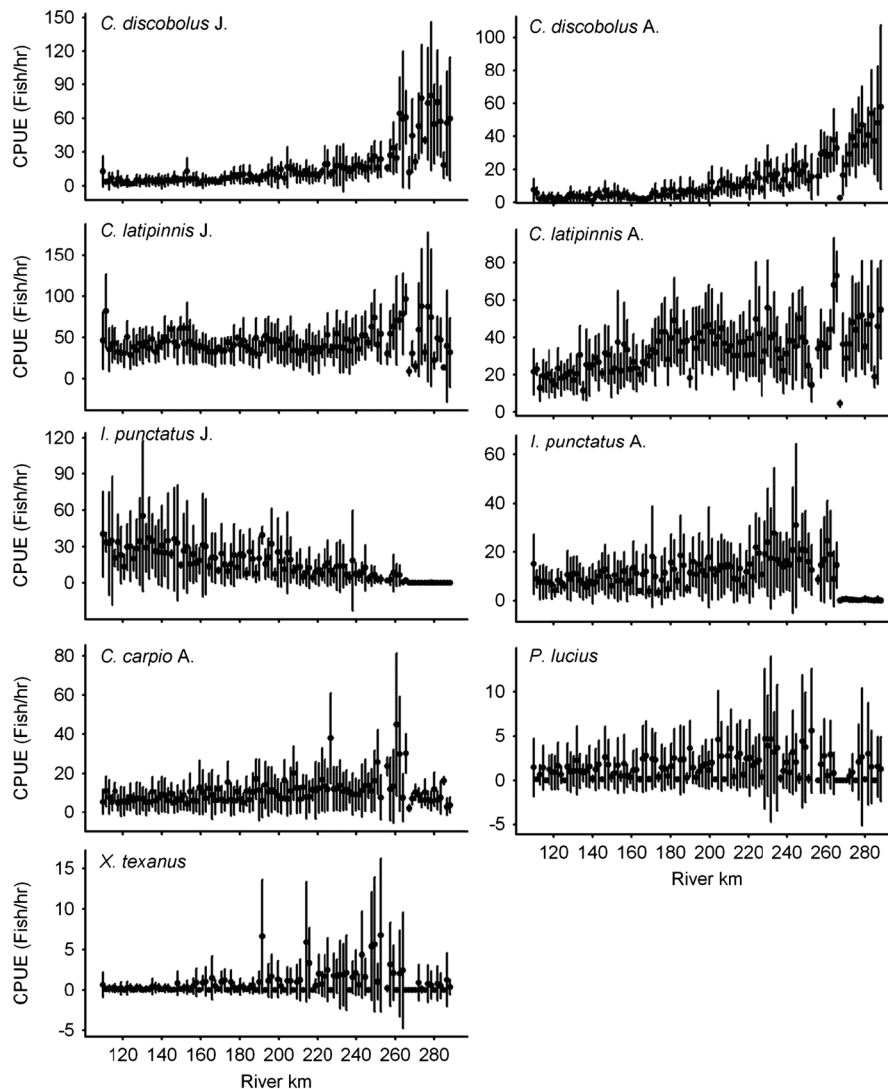
APPENDIX A

Figure A1. Mean (±1 S.D.) CPUE (fish/h) by Rkm for each species/age class investigated during the study period. Letters after species indicate juvenile (J.) or adults (A.)
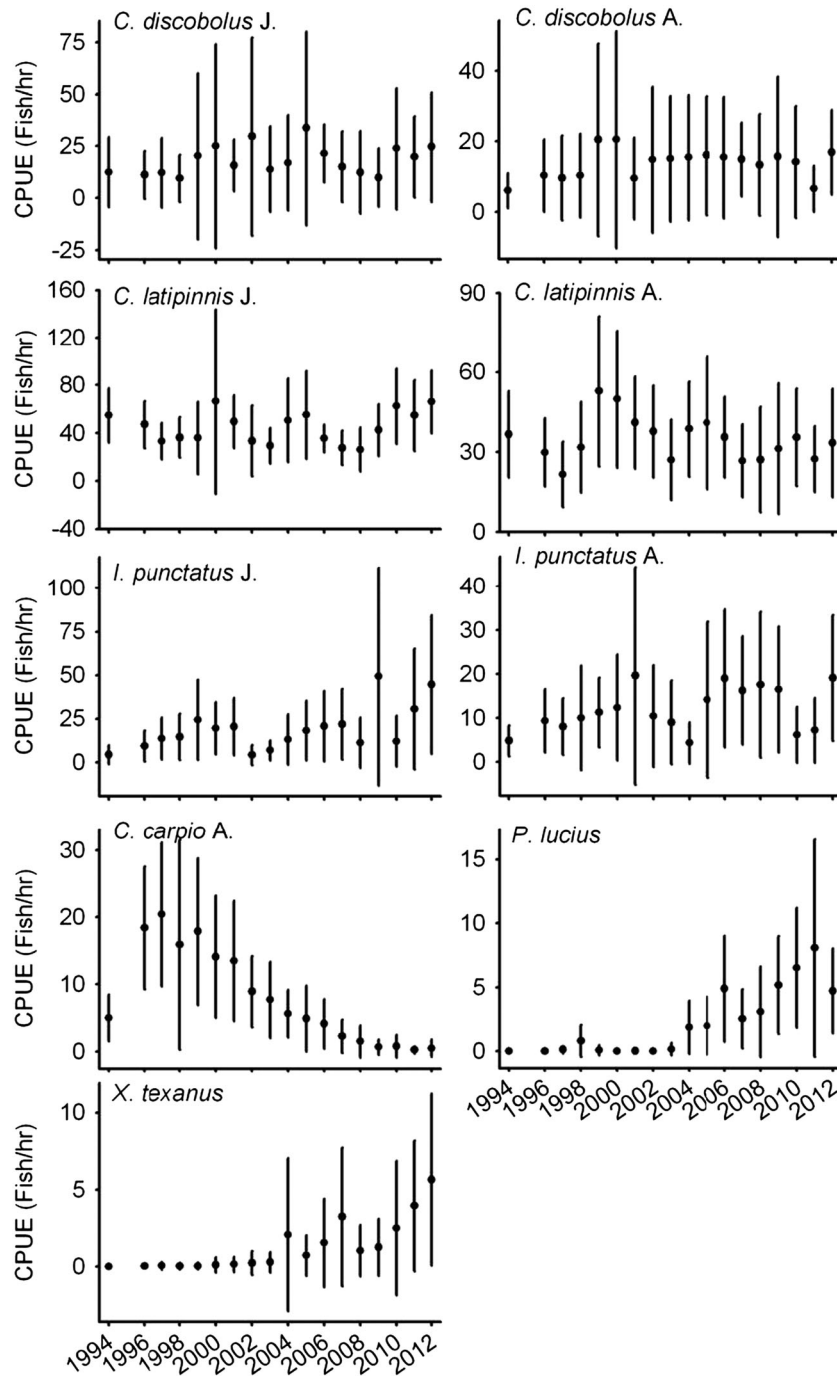
Figure A2. Mean (±1 S.D.) CPUE (fish/h) by year for each species/age class investigated during the study period. Letters after species indicate juvenile (J.) or adults (A.)
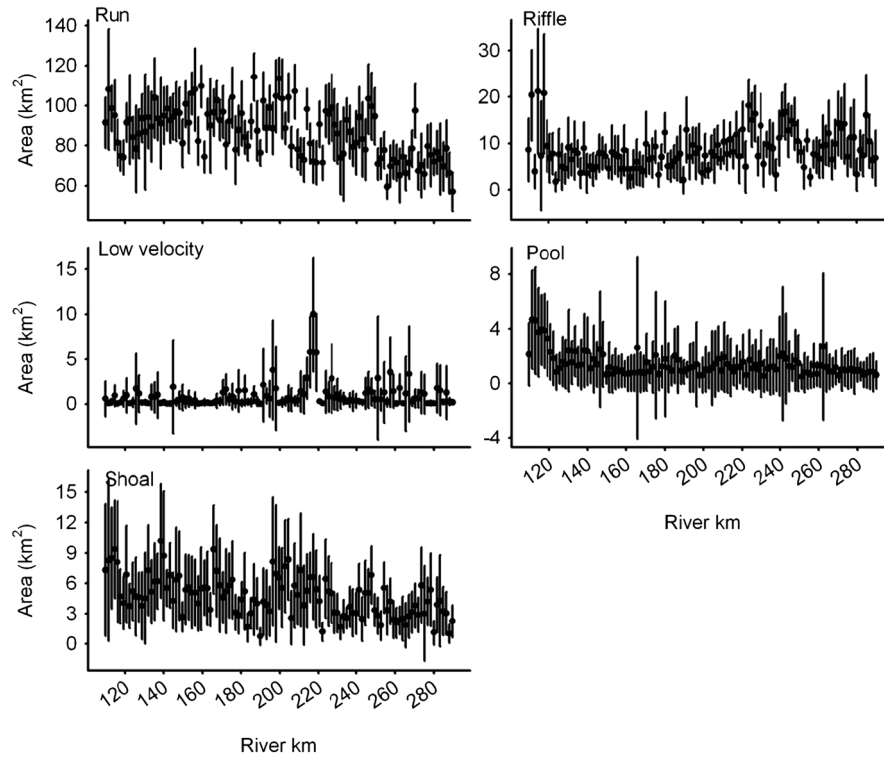
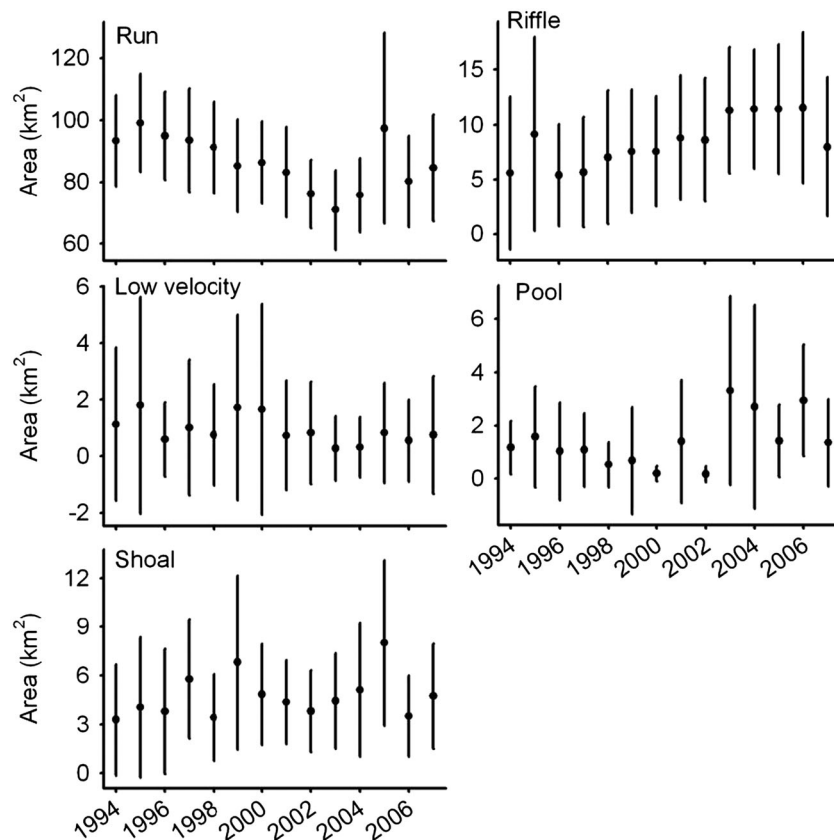Figure A3. Mean (±1 S.D.) area (km^2) of each mesohabitat type in each 1.6 Rkm between 1994 and 2007

Figure A4. Mean (±1 S.D.) area (km^2) of each mesohabitat type by year between 1994 and 2007